THE ANATOMY OF THE DECAPOD CRUSTACEAN AUXILIARY HEART

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An auxiliary heart is found in many decapod crustaceans at the anterior end of the dorsal median artery before the artery branches to supply the supraesophageal ganglion and the peripheral oculomotor and visual systems. Although the existence of this auxiliary heart had been noted earlier, when it was named the cor frontale (Baumann, 1917), very little information was provided beyond a description of the muscles involved (for review, see Maynard, 1960). The following is a more thorough account of the anatomy of the cor frontale in several decapods with particular emphasis on the neural elements of the system.

MATERIALS AND METHODS

Specimens of *Callinectes sapidus,* the American blue crab, and *Panulirus interruptus,* the Californian lobster, were used for the most complete dissections. Specimens of *Scylla serrata,* the Australian mud crab, and two Californian marine crabs, *Cancer productus* and *Cancer antennarius,* were also investigated.

The primary method used to trace the neural elements was *in vivo* methylene blue staining by perfusion through the dorsal medial artery. Fixation of the material so stained was done by the method of Pantin (1969). Light microscopic histological preparations of the heart nerves and tendon ganglia were made using glutaraldehyde fixation, Epon embedding and toluidine blue staining. Electron microscopy of the muscles was done with a 3% glutaraldehyde, 1% paraformaldehyde, collidine buffer, 1178 m osmol fixation and Epon embedding. To trace the course of vessels of the system, liquid latex (Connecticut Valley Biological Supply) was injected into the cerebral vascular system via the dorsal median artery.

RESULTS

The basic anatomy of the cor frontale, which is remarkably similar in all the decapods studied, is illustrated in Figures 1, 2, and 3. The blood flows anteriorly from the main heart through the dorsal median artery to supply the supraesophageal ganglion and the peripheral optic ganglia and oculomotor system (Fig. 1). Before the blood is distributed to these areas, it flows through the auxiliary heart. The anatomy of this heart can most conveniently be described by breaking it down into three elements: the blood vessels, the muscles and tendons, and the associated neural system.

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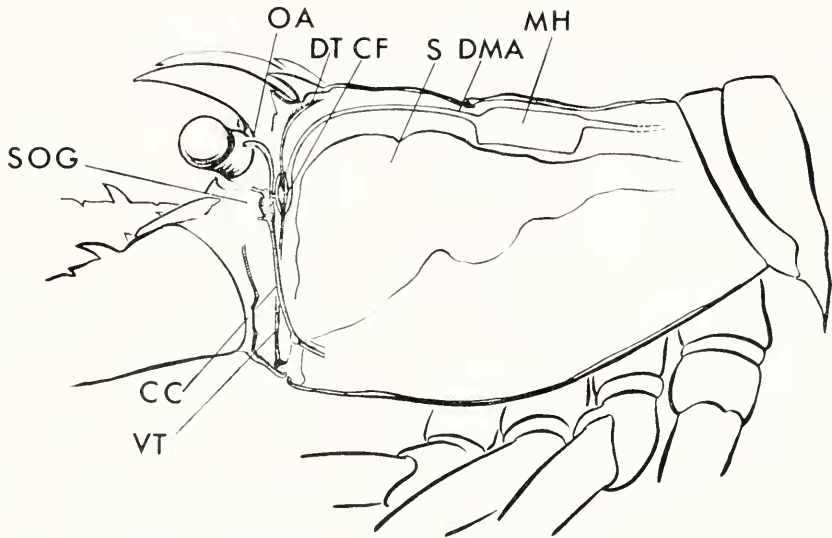
FIGURE 1. Overview of the location of the cor frontale (CF) in relation to other structures in the cephalothorax of the spiny lobster, *Panulirus interruptus*. Blood flows from the main heart (MH) through the dorsal median artery (DMA) over the stomach (S) to the cor frontale (CF) from which it exits to the eyecup via the ophthalmic artery (OA) and to the supraesophageal ganglion (SOG) via the cerebral artery (CA). Other abbreviations are: dorsal tendons of the cor frontale (DT); single ventral tendon (VT); and circumesophageal connectives (CC).

Blood vessels

The wall of the auxiliary heart is formed by the dilated terminal end of the dorsal median artery. Note (Figs. 2 and 3) that no muscle is contained in the wall of the artery itself. Rather, the wall of the cor frontale is composed of the same two layers as that of the dorsal median artery.

The course of the blood vessels from the cor frontale can be seen in the latex injected preparation of *Callinectes* in Figure 4. Blood enters the cor frontale sinus from the dorsal median artery and leaves via the cerebral artery which supplies the supraesophageal ganglion, a few small vessels which supply the nearby eyestalk muscles and the two large ophthalmic arteries which supply the visual and oculomotor system in the eyecup. (The dorsal median artery is sometimes referred to as the ophthalmic artery, a misnomer, since the true ophthalmic arteries, which run to the eyes, receive only part of the supply of the dorsal median artery.)

Muscles and tendons

The cor frontale muscles are two distinct strips of striated muscle originating from tendons outside the dorsal median artery. In the crab, the tendons begin as multiple insertions on the dorsal carapace just behind the middle cylinder of the eyestalk. This origin can be seen as two indentations on both the underside and on the external surface of the dorsal carapace. In the lobster, which has no

eyestalk middle cylinder, the tendons originate in an equivalent position on the dorsal carapace between the two large spines of the rostrum. Each of these two tendons is joined by an orthogonal lateral tendon before the tendons pass through the wall of the dorsal median artery. At this point, the cor frontale sinus begins (Fig. 2). As the tendons pass into the sinus they give rise to the two muscles
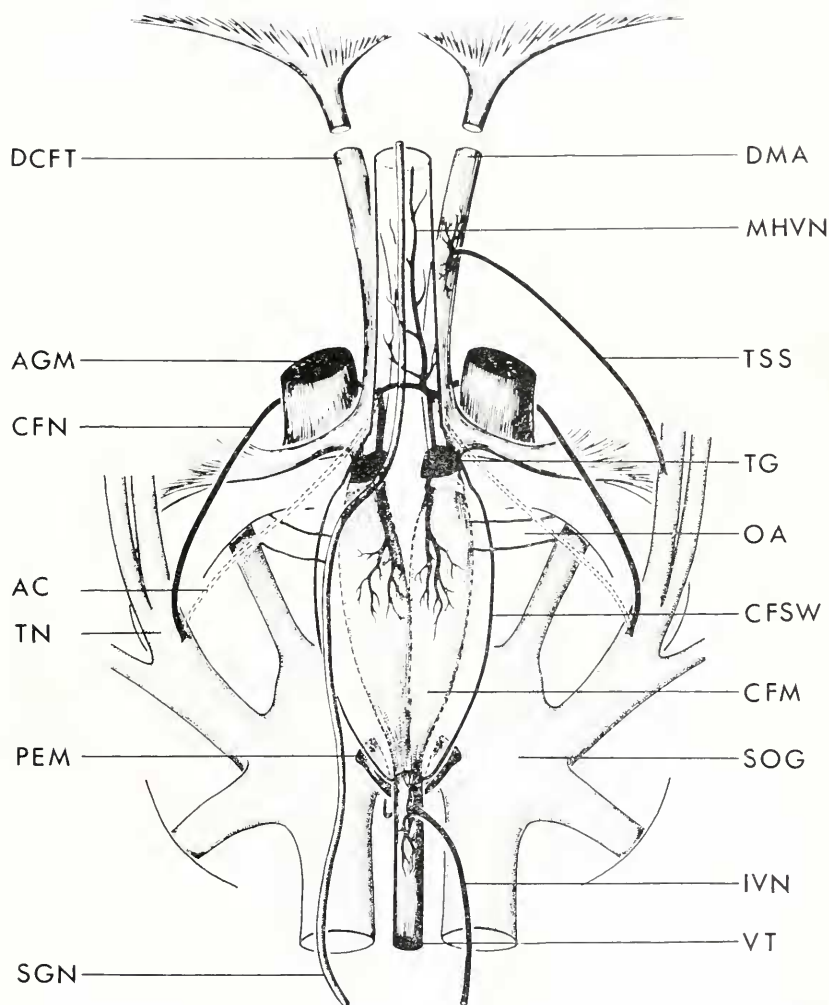

FIGURE 2. Transverse view of the cor frontale of *Panulirus interruptus*. Abbreviations are: dorsal cor frontale tendons (DCFT); anterior gastric muscles (AGM); cor frontale nerve (CFN); alternate course of the cor frontale nerve (AC); tegumentary nerve (TN); stomatogastric nerve (SGN); ventral tendon (VT); inferior ventricular nerve (IVN); posterior eyestalk muscles (PEM); supraesophageal ganglion (SOG); cor frontale muscles (CFM); cor frontale sinus wall (CFSW); ophthalmic artery (OA); tendon ganglion (TG); occasional separate tendon sensory supply (TSS); and nerve to main heart valve (MHVN); dorsal median artery (DMA).
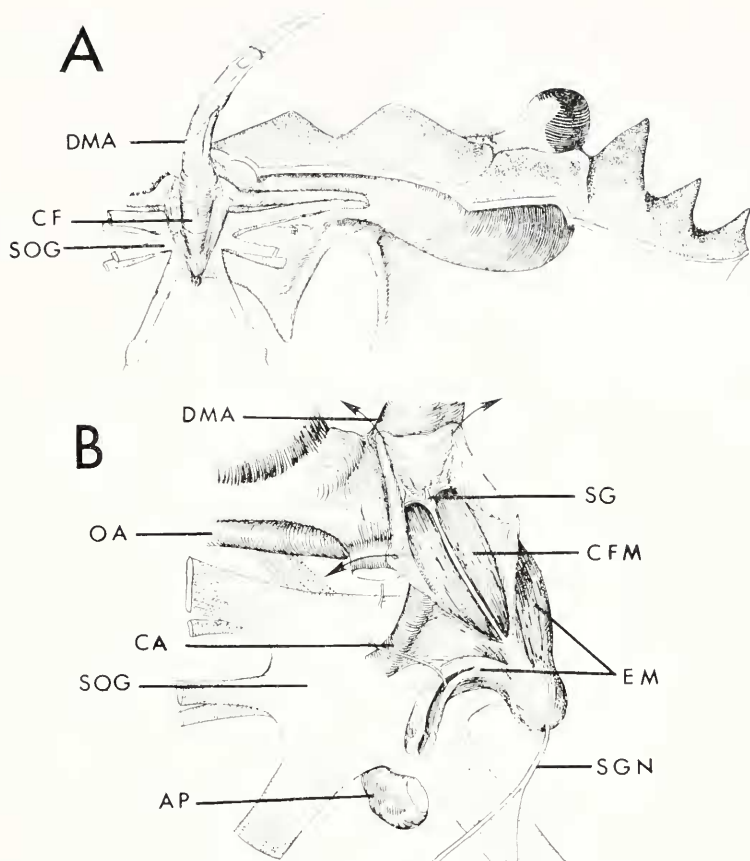
FIGURE 3. Transverse view of the cor frontale in cephalothorax of the *Callinectes sapidus*. A shows relation of cor frontale (CF) to cephalic structures. DMA indicates dorsal median artery entering the cor frontale. Muscles bordering cor frontale (EM) are the eyestalk muscles. The supraesophageal ganglion (SOG) lies under the cor frontale and receives its blood supply via the cerebral artery (CA). B shows enlarged view of center of (A) showing the cor frontale sinus walls opened at arrows to expose the enclosed cor frontale muscles (CFM) and stomatogastric ganglion (SG). The stomatogastric ganglion (SG) lies inside the cor frontale. SGN is the stomatogastric nerve exiting the cor frontale at the point where the tendon has been detached by dissection from its apodeme (AP).

of the cor frontale. These muscles extend the length of the sinus and exit at the ventral posterior end as a single tendon attached to an apodeme. This apodeme (Fig. 3), which arises from an epistome above the mouth, is a common attachment for the cor frontale muscles, the dorsal eyestalk muscles and several esophageal muscles.

The cor frontale of the lobster differs from that of the crab primarily in the extent of the development of the tendons. The dorsal tendons of the lobster are much larger and the single ventral tendon is greatly elongated. These differences are consistent with both the larger size and the dorso-ventral elongation

of the lobster cephalothorax (Fig. 1). The size of the tendons is particularly striking in view of the relatively small size of the cor frontale muscles. Associated with these tendons is a well developed sensory innervation.

There are around one hundred individual muscle fibers in a cross section of the muscle (Fig. 5). At two points on the muscle perimeter are areas which contain much connective tissue, large motor axons and some fibers which contain dense granules also seen in the tendon ganglia. The muscles of the cor frontale are striking in their compactness and white hue, being distinctly whiter and more dense than the fastest portions of the eyestalk muscles which border them. The preliminary electron microscopy which was done shows only a few small mitochondria which may account for the whiteness of the muscle. The banding pattern of the sarcomeres is not well defined. The Z band is moderately dense and appears to be continuous across the sarcomere. The sarcoplasmic reticulum is scarce and connections with the well-developed T tubular system are rare. The appearance is that of a crustacean somatic, rather than heart, muscle; and, in fact, it has been suggested that the cor frontale muscles are somatic muscles secondarily adapted for cardiac function (Maynard, 1960).

Neural anatomy

Cor frontale nerve. This nerve, which is the neural connection between the auxiliary heart and the supraesophegeal ganglion, exits from the supraesophageal ganglion with the tegumentary nerve and splits off as a small diameter branch to curve back and up to the dorsal aspect of the cor frontale. The nerve passes under the cor frontale tendon to enter the dorsal median artery near the entry of the tendon.

In the lobster, the cor frontale nerve either leaves the tegumentary nerve close to the ganglion and takes a direct route to the heart (dashed line in Fig. 2), or more commonly, it continues with the tegumentary nerve up to the anterior gastric muscle where it leaves the tegumentary nerve and passes around the gastric muscle to enter the dorsal aspect of the artery. In the crab, the course of the nerve through the cephalothorax is invariant but quite long and difficult to trace. It leaves an anterior branch of the tegumentary nerve laterally and curves back to the cor frontale as a fine nerve embedded in the dorsal hypodermis.

Cross section of the cor frontale nerve shows seven fibers. After methylene blue staining one may observe two large axons which can be traced to the cor frontale muscles, one large axon which runs out the dorsal median artery to the valve of the main heart (see below) and several small axons whose origin and termination could not be determined because of their poor staining. The motor neuron somata of the fibers supplying the cor frontale muscles and main heart valve originate in the supraesophageal ganglion. This was shown by electrophysiological recording and by methylene blue staining in which the two fibers can be traced clearly from the ganglion to innervate the muscles. Attempts to back fill the somata with cobalt or procion yellow have, to date, been unsuccessful.

In the lobster and crab, motor axons to the heart muscle split into two branches as the nerve enters the artery. One branch supplies the ipsilateral muscle and the other passes across the artery to join with the axons of the contralateral cor
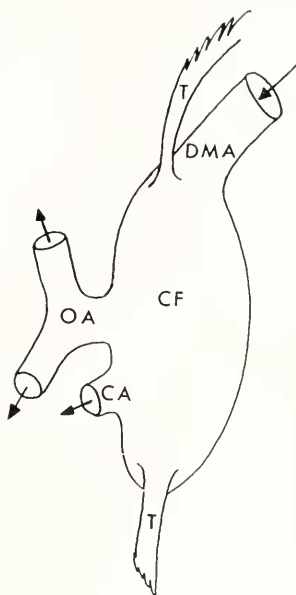
FIGURE 4. Sketch of a liquid latex injected cast of *Callinectes sapidus* cor frontale. Blood flows via the dorsal median artery (DMA) into the cor frontale (CF) and out via the cerebral artery (CA) and the ophthalmic artery (OA). Dorsal and ventral tendons (T) of the cor frontale muscles are shown exiting the cor frontale sinus.

frontale nerve to supply the contralateral muscle. Since the same motor axon splitting occurs on both sides, the result is that each muscle is innervated by four axons, two from each half of the supraesophageal ganglion.. In the lobster, this crossing of the motor axons forms a distinct central neural cross bar structure which is embedded in the dorsal wall of the artery near the tendons. In the crab, when the two cor frontale nerves enter the artery, they do not form the distinct neural cross bar structure seen in the lobster. The same splitting and crossing over of the motor axons occurs, but at lower level closer to the muscles.

Main heart valve nerve. In the lobster and crab, a single axon from each cor frontale nerve joins a contralateral partner near the right dorsal tendon to form a nerve which turns away from the cor frontale and, embedded in the arterial wall, travels the entire length of the dorsal median artery. The two axons innervate the valve of the artery as the latter leaves the main heart. Histological sections of the nerve in the lobster show two large axons and three much smaller axons. The two large axons stain darkly with methylene blue and clearly go directly to and end in the arterial valve. The others stain poorly with methylene blue and branch repeatedly in the arterial wall. The three small fibers may be a sensory system which supplies the arterial wall since the wall contains no muscle.

The valve of the dorsal median artery at the main heart has two components. One, a well developed semilunar valve with cusps opening to the arterial side which appear to operate passively to prevent backflow and the other, a circular ring of muscle fibers between the valve and the heart muscle proper. It is this

circular muscle which the two axons innervate. As the two axons approach the valve, each axon splits first into two and then into four branches. Two branches of each axon charactistically cross the midline of the valve so that each half of the circular muscle ring is supplied by axons from both halves of the supraesophageal ganglion. The axons terminate in an extensive plexus among circular muscle fibers of the valve.

In a transilluminated methylene blue stained preparation, these muscle fibers are quite distinct from those of the main heart muscle and appear similar to those described by Alexandrowicz (1932) in several crustacean heart valves. From their termination on the circular muscle of the valve and the lack of any other nerve supply to these muscles, it is assumed that the axons to the valve are motor.

Cor frontale tendon ganglia. Tightly adhering to the upper tendon of each cor frontale muscle as it passes through the arterial walls is an ill-defined aggregation of neural tissue here termed the tendon ganglia (Fig. 2). The motor axons to the muscles pass directly through this ganglion and cannot be easily separated from it. In light microscopic toluidine blue stained sections of the ganglion, several distinct types of somata are found. Two of these somata types contain numerous either large or small darkly stained granules suggestive of neurosecretory vesicles. A third class of somata exhibits a clear cytoplasm and distinct nucleus. Numerous neural processes are also seen in the ganglia, some of which contain the same granules seen in the somata. These processes do not appear to form a distinct neuropile, although there is a somewhat circular course of the fibers within the ganglion. The density of the ganglion excludes its function as a neurohaemal organ. Several types of fibers enter or leave the tendon ganglia. There are many small fibers which can be traced from the ganglia to extensive ramifications in the arterial wall. The arterial and cor frontale sinus walls are innervated by fibers which appear to terminate in the tendon ganglia. Also associated with the tendon ganglia are fibers which, when stained with methylene blue, can be seen to branch extensively over the upper tendons of the cor frontale muscles. These fibers are presumed to be sensory, since they are never found extending beyond the tendon to the muscle. All these above fibers are very fine and their termination difficult to follow. In the lobster, the tendon sensory fibers sometimes go directly to the supraesophageal ganglion via a separate sensory nerve which joins the tegumentary nerve above the origin of the cor frontale motor nerve (Fig. 2).

Finally, connections can sometimes be traced between the stomatogastric nerve and the tendon ganglia. In the lobster the stomatogastric ganglion is located inside the dorsal median artery where this artery passes over the stomach (a few centimeters posterior to the cor frontale). The nerve then exits from the artery but adheres to it, giving off many small branches, one of which can sometimes be traced to the tendon ganglia or to the nerve carrying the axon to the main heart valve. In the crab, the stomatogastric ganglion is enclosed within the sinus of the cor frontale directly between the two muscles (Fig. 3). Two lateral nerves from this ganglion leave the sinus to supply the anterior gastric muscles. These gastric nerves leave the sinus near the cor frontale tendons and give off fine branches to the tendon ganglia. The stomatogastric ganglion inside the cor frontale appears to be the same ganglion referred to as the ventricular ganglion (Baumann, 1917; Maynard, 1960).

Ventral tendon sensory units. On the single long ventral tendon of the lobster a distinct sensory innervation is found which extends down the tendon. The fibers from this nerve enter the inferior ventricular nerve. The inferior ventricular nerve, after leaving its origin in the supraesophageal ganglion, passes through an opening in the cor frontale tendon. The sensory units from the tendon join the nerve and travel toward the inferior esophageal ganglion. In the crab, the ventral tendon is very short (Fig. 3), and the inferior ventricular nerve does not pass through the tendon. No sensory fibers comparable to those of the lobster ventral tendon have been found in the crab.

Auxiliary heart in the eyecup. When the oculomotor muscles in the eyecups are exposed by dissection (while the ophthalmic arteries are inflated by saline perfusion or by liquid latex injection), muscle number 21 (nomenclature of Cochran, 1935) is found to lie within the arterial lumen and shows anatomical features similar to the cor frontale. This is most obvious with the latex injection when the latex is found within the lumen of the artery completely surrounding the muscle. The muscle divides easily into two sections. Part of the muscle has the appearance of the other eyecup muscles and the rest has the white dense appearance of the cor frontale muscles.

The presence of this muscle in the lumen of the blood vessel, its physical resemblance to the cor frontale muscle and its location within the arterial lumen immediately before the artery enters the neuropile of the eyecup indicate that it may be another auxiliary heart. The optic neuropile, like the supraesophageal ganglion, but unlike most crustacean ganglia, requires a constant blood supply and fails soon after this flow is interrupted. This muscle has been noted before to be "heavily vascularized" (Sandeman, 1967), but its presence inside the vessel lumen and possible auxiliary heart function were not noted. In the shrimp, *Palaemon*, an eyecup muscle inserted in the ophthalmic artery has been described and a blood pumping function ascribed to it (Debaisieux, 1944; Demal, 1953).

DISCUSSION

The term auxiliary heart, rather than accessory heart (Maynard, 1960), has been used here for the cor frontale, since its fine structure and electrophysiological reflex response (Steinacker, 1978) suggest a phasic function which is recruited only when the main heart activity is insufficient for the circulatory requirements of cerebral nervous system. The anatomy of this heart reveals a complex organ whose function appears to be controlled by and integrated with several other systems. From anatomical and electrophysiological evidence (Steinacker, 1978), the main integrative center appears to be in the supraesophageal ganglion where the motoneurons are located. The tendon ganglia may be a second, local integrative center, with perhaps a neurosecretory function whose control could be exerted at two sites; as a direct action of neurosecretory products on the muscle and/or by a central effect on the neurons in the supraesophageal ganglion. Since blood flows past the tendon ganglia to the supraesophageal ganglion, neurosecretory products will be carried directly to a central integrative system in the supraesophageal ganglion. In addition, afferent or interneuronal fibers from the tendon ganglia may travel in the cor frontale nerves to or from the tendon ganglia and the

supraesophageal ganglion. There are at least four fibers in the cor frontale nerves which are not motor and which may arise all or in part from the tendon ganglia.

The involvement of the stomatogastric ganglion with an auxiliary heart deserves mention. In a decapod with an open venous system and inflexible carapace, variations in volume of a highly distensible stomach will have a considerable influence on blood pressure. In addition to the passive influence of stomach volume on blood pressure, active uptake of salt and water by the gut in crustaceans has been demonstrated (Weisman, 1874; Fox, 1952; Croghan, 1958). The stomatogastric system may be involved in hemodynamics through the passive effect of the stomach volume on blood pressure and through active control of salt and water uptake. The stomatogastric system and cor frontale also have a possible neural communication via the supraesophageal ganglion and lower control centers. Evidence is building for a common control center (or centers) for the gills, main heart, auxiliary heart and stomatogastric system. Excitatory and inhibitory fibers, which have been found in the circumesophageal connectives, govern these systems (Wiersma and Novitski, 1942; Mendelson, 1971; Field and Larimer, 1975; Wilkens, Wilkens, and McMahon, 1974; Steinacker, 1978). Command fibers for the stomatogastric system are thought to originate in the supraesophageal ganglion (Dando and Selverston, 1972) and neurosecretory cells connecting the supraesophageal and lower neural centers exist (Goldstone and Cook, 1971).

The sensory innervation of the tendons of the cor frontale introduces the possibility of either feedback control or coordination of cor frontale function with the other cardioregulatory systems. In the case of the ventral tendon, this infor-
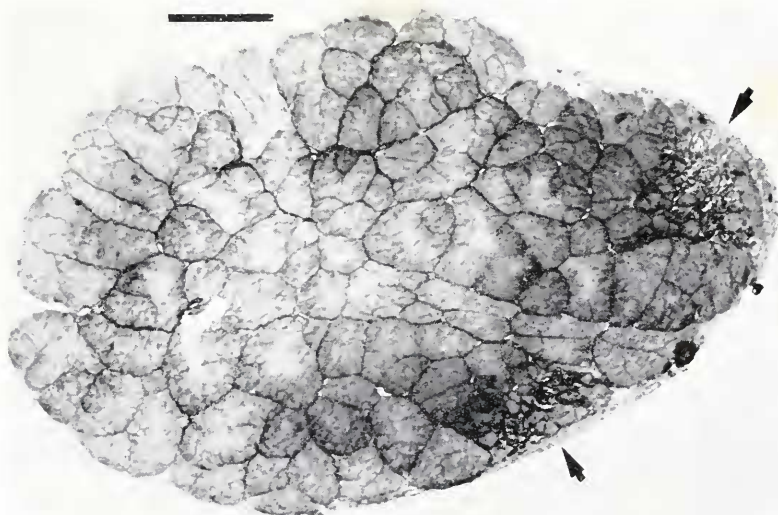

FIGURE 5. Light micrograph of transverse section of a single cor frontale muscle illustrating somatic nature of the muscle. Note small number of homogeneous fiber types with the exception of two areas (at arrows) where small muscle fibers, nerve fibers and connective tissue stroma is found. Scale equals 100 microns.

mation appears to be feeding into the esophageal and/or stomatogastric system since the sensory fibers travel away from the supraesophageal ganglion. In the dorsal tendons, either the tendon ganglia and/or the supraesophageal ganglion receive the sensory input from the tendons. In addition, the innervation of the walls of the artery and the sinus wall of the cor frontale may provide direct information on blood pressure levels which could be used by either the supra-esophageal ganglion or the tendon ganglia.

The nerve which carries the two axons to the main heart valve from the supraesophageal ganglion appears to be the often cited nerve of Lemoine (Lemoine, 1868) or nervus cardiacus anterior (Police, 1908; Alexandrowicz, 1932; and Health, 1941), which was believed by them to originate in the stomato-gastric ganglion. However, in all the decapods examined in the present study, these two axons, stained darkly by methylene blue, could be followed clearly from the supraesophageal ganglion in the cor frontale nerve down the length of the dorsal median artery to the main heart valve where they provide the sole innerva-tion of the valve. The wall of the dorsal median artery along its entire length is a meshwork for fine nerve fibers, some of which can be traced to the stomato-gastric nerve and others to the nerve in which the two axons run to the heart valve. In some cases, distinct connections could be found between the stomato-gastric nerve and the nerve from the cor frontale carrying the two axons to the heart valve. These connections may be the source of error as to the origin of the heart valve axons in the earlier literature.

It may appear strange that such a well developed system as the cor frontale has previously escaped detailed attention, particularly in view of the wide interest in crustacean neurophysiology. The muscles are fairly conspicious, although they had been previously been confused with the eyestalk muscles judging from their inclusion in the eyestalk numbering system and the name, musculi oculi basilis posterior, applied to them (Cochran, 1935). However, the small size and circuitous route of the nerves from the supraesophageal gauglion to the cor frontale and the diffuseness of the system (in comparison to the simplicity of the main heart) may also explain the neglect. In addition, electrophysiological work on the supraesophageal ganglion in an isolated preparation has been hampered by the lack of proper perfusion techniques (Steinacker, 1975) and so (with the excep-tion of recording from intact animals) the cephalic portion of the decapods has been relatively unexplored in comparison to the extensive work on more pe-ripheral crustacean ganglia.

Summary

The anatomy of an auxiliary heart found in many decapod crustaceans is described. This heart is found at the anterior end of the dorsal median artery

before the artery divides to supply the cerebral nervous system. The heart is essentially two strips of modified somatic muscle located inside a sinus in the dorsal median artery. These muscles are innervated by four motoneurons located in the supraesophageal ganglion. Sensory innervation and possible neurosecretory elements are also described.

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